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A new classification of the Chirostyloidea (Crustacea: Decapoda: Anomura)

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Abstract

The high level classification of the Chirostyloidea Ortmann, 1892, is reviewed. Eumunididae Milne-Edwards & Bouvier, 1900, is resurrected for two genera formerly placed in the Chirostylidae Ortmann, 1892, *Eumunida* Smith, 1883, and *Pseudomunida* Haig, 1979*,* based on shared characteristics such as the dorsal carapace striation, presence of supraocular spines of the rostrum, dentition of the mandible, presence of an epipod and an annulated exopod flagellum of maxilliped 1. Three families are now included in the Chirostyloidea: Chirostylidae, Eumunididae and Kiwaidae. Diagnoses are provided for each family as well as a key to the families. The fossil record of the Chirostyloidea is discussed, with putative records of *Eumunida* in the fossil record referred to the galatheid genus *Sadayoshia* Baba, 1969.

Key words: Galatheoidea, Chirostylidae, Eumunididae, Kiwaidae, adult somatic morphology, larval morphology, fossil record

Introduction

Recent focus on the phylogeny of Anomura has generated significant molecular phylogenetic information that has challenged the traditional understanding of the marine squat lobsters and porcelain crabs, the Galatheoidea, which comprised the Chirostylidae Ortmann, 1892, Galatheidae Samouelle, 1819, Porcellanidae Haworth, 1825, and Kiwaidae Macpherson, Jones & Segonzac, 2005 (e.g., Ahyong *et al.* 2009; Bracken *et al.* 2009). Most importantly, the Galatheoidea have been shown to be polyphyletic, warranting the removal of the Chirostylidae and Kiwaidae to a separate superfamily, Chirostyloidea (Schnabel *et al.* in press; Ahyong *et al.* in press).

The family Chirostylidae currently includes seven genera and over 200 species worldwide (Baba 2009; Baba & Lin 2008; Baba *et al.* 2008; Schnabel 2009). The chirostylid genera fall into two, apparently natural, groups. One group comprises *Chirostylus* Ortmann, 1892, *Gastroptychus* Caullery, 1896, *Hapaloptyx* Stebbing, 1920, *Uroptychodes* Baba, 2004, and *Uroptychus* Henderson, 1888. The second group includes *Eumunida* Smith, 1883, and *Pseudomunida* Haig, 1979. These two groups were first recognised by A. Milne-Edwards & Bouvier (1894) based on somatic morphology, who informally named the first 'Diptyciens', which contained *Ptychogaster* (now *Gastroptychus*) and *Diptychus* (now *Uroptychus*), and the second 'Eumunidiens', for *Eumunida*. Several new chirostylid genera have been recognized since 1894. Stebbing (1920) described *Hapaloptyx* for a new species, *H. difficilis*. *Hapaloptyx* is poorly known at present, but is most similar to *Chirostylus*. Haig (1979) erected *Pseudomunida* for a new species, *P. fragilis*, a species having close morphological affinities to *Eumunida*, and corresponding to the 'Eumunidiens' group. *Uroptychodes* was erected for *U. epigaster* Baba, 2004, and related species formerly placed in *Uroptychus* (Baba 2004). Recent studies of sperm and larval morphology also support this distinction between groups (e.g., Clark & Ng 2008; Guerao *et al.* 2006; Tudge 1997). Likewise, the two groups appear to have differing life histories, with *Eumunida* producing small eggs in which larvae hatch at an early stage of development (larvae are not currently known for *Pseudomunida*). In contrast, species of the remaining chirostylid genera produce large

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eggs with abbreviated development (Clark & Ng 2008; Pike & Wear 1969). That two distinct morphological groups exist within Chirostylidae is thus clear, having support from somatic morphology and from what is known of life history. However, the question remains as to whether these groups are sister clades.

Two main hypotheses have been proposed about internal phylogenetic relationships within the Chirostyloidea. Ahyong *et al.* (2009) and Schnabel *et al.* (in press), using ribosomal sequences, recovered a chirostyloid clade in which *Kiwa, Eumunida* and *Pseudomunida* formed a paraphyletic relationship outside of a robust 'Dypticiens' clade. Among these, *Eumunida* was strongly supported as close to other chirostylids, but the positions of *Kiwa* and *Pseudomunida* were ambiguous owing to low nodal support. Using nuclear protein coding gene sequences, however, Chu *et al.* (2009) and Tsang *et al.* (in press) found strong nodal support for a *Eumunida* + *Kiwa* clade as sister to the main chirostylid clade (*Pseudomunida* was not analysed). The results of each of these analyses differ in some details of topology, but the relationships at the well-supported nodes are compatible. Thus, according to all analyses, the Chirostylidae *sensu lato* are not monophyletic. The sum of evidence indicates that the two chirostylid groups first recognised by A. Milne-Edwards & Bouvier (1894) form separate clades, of which one, the Eumunidiens group is closer to Kiwaidae than to other chirostylids. Thus, we herein recognise a separate family within the Chirostyloidea, Eumunididae, to accommodate *Eumunida* and *Pseudomunida* (Fig. 1).

Material and methods

Specimens used are deposited in the collections of the Australian Museum (AM), National Institute of Water and Atmospheric Research (NIWA), the National Museum of New Zealand Te Papa Tongarewa (NMNZ) and the Muséum national d'Histoire naturelle, Paris (MNHN). Postorbital carapace length (pcl) is given in millimetres (mm). Drawings were made using a WACOM Intuous3 Graphics Tablet and Adobe Illustrator CS3.

Systematics

Order Decapoda

Chirostyloidea Ortmann, 1892

Diagnosis. Body symmetrical, carapace with or without transverse striae; rostrum variously developed, usually prominent; supraocular spines present or absent. Sternal plastron consisting of sternites 3–7. Thoracic somite 8 without sternal plate. Abdomen well developed, all somites sclerotized, articulating. Tailfan well developed, folded against preceding somite; telson and uropods laminar. Telson transversely divided by suture. Antennal peduncle consisting of 5 articles; acicle present or absent. Mandible with toothed cutting edge. Maxilliped 1 with or without epipod. Pereopod 1 always chelate. Pereopod 2–4 as walking legs. Maxilliped 3 and pereopods without epipods. Gills phyllobranchiate.

Composition. Chirostylidae Ortmann, 1892, Eumunididae A. Milne Edwards & Bouvier, 1900, Kiwaidae Macpherson, Jones & Segonzac, 2005.

Key to families of Chirostyloidea

1. Eyes vestigial. Mandibular cutting edge chitinous. Sternite 3 strongly produced anteriorly to an acute point............. ....Kiwaidae
- Eyes well developed. Mandibular cutting edge calcified. Sternite 3 anterior margin not strongly produced anteriorly, transversely sinuous, irregular or obtusely angled..........2
2. Carapace without transverse striae. Supraocular spines absent. Anterolateral margin of abdominal somite 2 without

anterolaterally directed spine. Maxilliped 1 without epipod. Male pleopod 1 present .... Chirostylidae
- Carapace with transverse striae. Supraocular spines present. Anterolateral margin of abdominal somite 2 with prominent, anterolaterally directed spine. Maxilliped 1 with epipod. Male pleopod 1 absent. ....Eumunididae

Chirostylidae Ortmann, 1892
(Fig. 2C–F, I–L)

Diptycinés A. Milne-Edwards & Bouvier, 1894: 296, 312; 1897: 116 [vernacular name, unavailable].
Diptyciens A. Milne-Edwards & Bouvier, 1894: 299. — Bouvier, 1896: 312 [vernacular name, unavailable].
Diptycinae Bouvier, 1896: 312. — A. Milne-Edwards & Bouvier, 1899: 71, 87; 1900: 350.
Chirostylidae Ortmann, 1892: 244.
Uroptychidae Alcock, 1901: 236, 278.

Diagnosis. Carapace surface smooth, tuberculate or spinose but without transverse striae, posterolateral margin not distinctly defined or greatly inflated; rostrum variously shaped; supraocular spines absent. Anterolateral margin of abdominal somite 2 without prominent, anterolaterally directed spine. Sternite 3 not strongly produced anteriorly. Eyes well developed. Basal antennular article with distolateral spines. Antennal peduncle consisting of 5 articles; acicle present or absent. Mandibular cutting edge calcified, strongly serrated along its length. Maxilliped 1 without epipod; exopod flagellum present or absent, not annulated. Maxilliped 3 to pereopod 4 each with 2 arthrobranchs (well-developed or vestigial on maxilliped 3). Pereopod 5 with 1 arthrobranch only. Pereopods 2–4 with pleurobranch. Male pleopods 1 and 2 present. Male pleopods 3–5 vestigial or absent.

Type genus. *Chirostylus* Ortmann, 1892, by original designation.

Composition. *Chirostylus* Ortmann, 1892, *Gastroptychus* Caullery, 1896, *Hapaloptyx* Stebbing, 1920, *Uroptychodes* Baba, 2004, *Uroptychus* Henderson, 1888.

Remarks. Pleopods 3–5 are absent in most male chirostylids, but are vestigial in some species of *Gastroptychus* (e.g., *G. rogeri* Baba, 2000, and *G. investigatoris* (Alcock & Anderson, 1899), K. Baba, pers. com.; AM P53251, *G. rogeri*).

Eumunididae A. Milne Edwards & Bouvier, 1900, stat. nov.
(Fig. 1, 2A, B, G, H)

Eumunidiens A. Milne-Edwards & Bouvier, 1894: 299, 308, 312. — Bouvier, 1896: 312. — A. Milne-Edwards & Bouvier, 1897: 8, 116 [vernacular name, unavailable].
Eumunidae A. Milne-Edwards & Bouvier, 1900: 364.

Diagnosis. Carapace cordiform, elongate, with transverse striae; posterolateral margin entire, not excavated; rostrum spiniform, flanked by mesial and usually also lateral supraocular spines; lateral supraocular spine well developed (*Eumunida*), minute or obsolete (*Pseudomunida*). Cervical groove distinct. Basal article of ocular peduncle obscured in dorsal view by rostral and supraocular spines. Anterolateral margin of abdominal somite 2 with prominent anterolaterally directed spine. Sternite 3 anterior margin transversely sinuous or irregular, not strongly produced anteriorly. Eyes well developed. Basal antennular article unarmed. Antennal peduncle consisting of 5 articles; acicle present. Mandibular cutting edge calcified, tridentate, with tooth at either end and single median tooth. Maxilliped 1 with well-developed epipod; exopod flagellum annulated in distal portion. Maxilliped 3 to pereopod 4 each with 2 arthrobranchs (vestigial on maxilliped 3). Pereopod 5 with 1 arthrobranch only. Pereopods 2–4 with pleurobranch. Male pleopod 1 absent. Male pleopod 2 vestigial or absent. Male pleopods 3–5 present or absent.

Type genus. *Eumunida* Smith, 1883, by monotypy.

Composition. *Eumunida* Smith, 1883, *Pseudomunida* Haig, 1979.

Remarks. The Eumunidiens group of A. Milne-Edwards & Bouvier, 1894, was used in the vernacular sense and as such is an informal name and not available under the International Code of Zoological Nomenclature (see Ng *et al.* 2008 for discussion of vernacular names as used by A. Milne-Edwards and Bouvier). However, A. Milne-Edwards & Bouvier (1900), regarding *Eumunida* as belonging to a Tribe within the Diptycinae, used the Latinized form, Eumunidae, and thus validated the name. Eumunidae has not since been used. In now recognising a separate family, Eumunididae, for *Eumunida* and *Pseudomunida*, we attribute authorship to A. Milne-Edwards & Bouvier (1900).

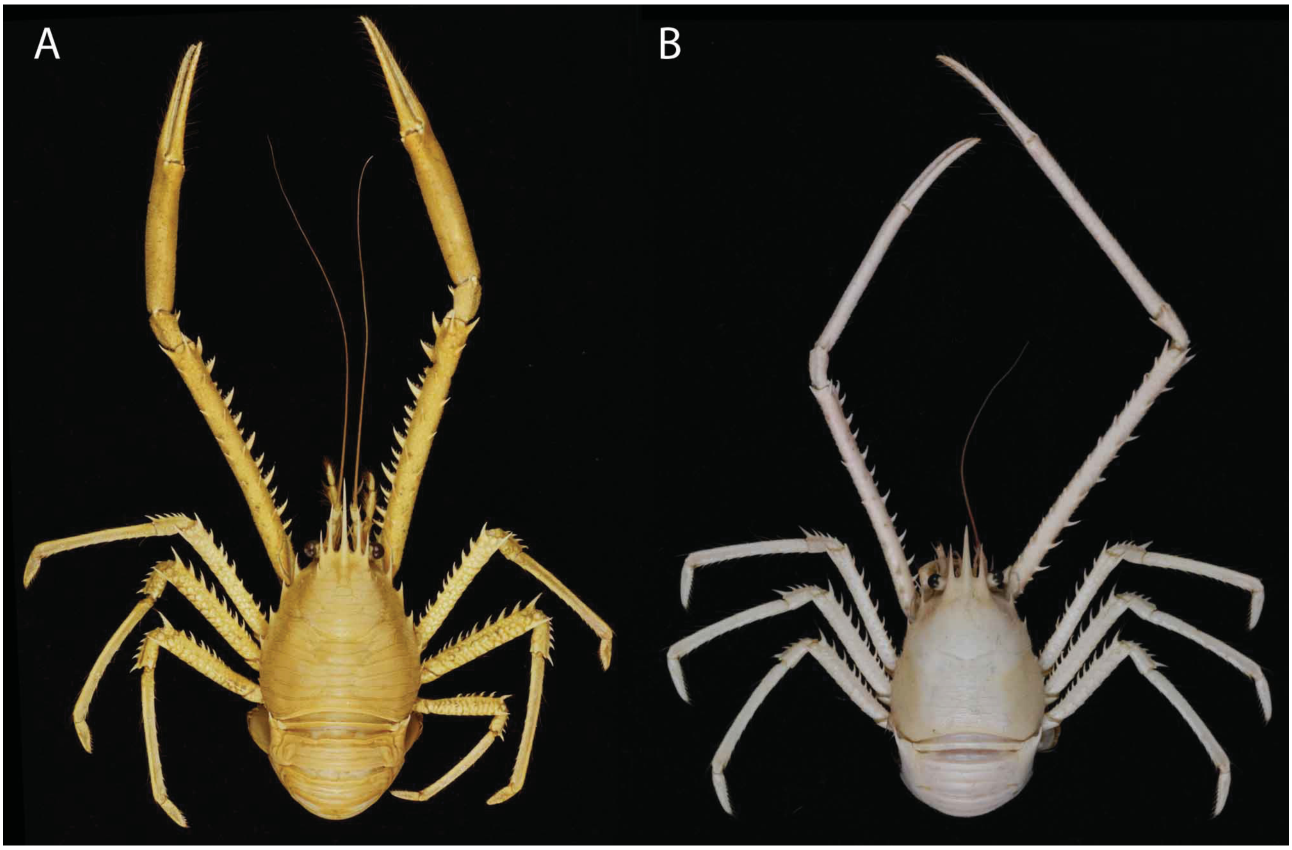

FIGURE 1. Eumunididae: A, *Eumunida australis* de Saint Laurent & Macpherson, 1990 (♀, pcl 52 mm, NMNZ Cr.5917); B, *Pseudomunida fragilis* Haig, 1979 (♀ ovig., pcl 20.5 mm, MNHN-Ga7507).

Kiwaidae Macpherson, Jones & Segonzac, 2005

Kiwaidae Macpherson, Jones & Segonzac, 2005: 712.

Diagnosis. Body elongate, symmetrical. Carapace smooth, without striae. Rostrum well developed, triangular. Cervical grooves clearly distinct; either side of mesogastric region with small, sharply defined pit. Abdominal somites smooth, anterolateral margin of abdominal somite 2 without anterolaterally directed spine with median transverse suture and longitudinal suture in the posterior half of telson. Sternite 3 strongly produced anteriorly to an acute point. Eyes strongly reduced, soft, not calcified, movable, unpigmented. Basal antennular article unarmed. Antennal peduncle consisting of 5 articles; acicle absent. Mandibular cutting edge chitinous, strongly serrated along its length. Maxilliped 1 with well-developed epipod; exopod flagellum not annulated. Cheliped (pereopod 1) with dense corneous spinules along distal portion of occlusal margin. Pereopod 5 inserted below sternite 7, insertion not visible ventrally. Maxilliped 3 to pereopod 4 each with 2 arthrobranchs (vestigial on maxilliped 3). Pereopod 5 without arthrobranch. Pleurobranchs absent. Male pleopods 1–5 present.

Type genus. *Kiwa* Macpherson, Jones & Segonzac, 2005, by monotypy.

Composition. *Kiwa* Macpherson, Jones & Segonzac, 2005.

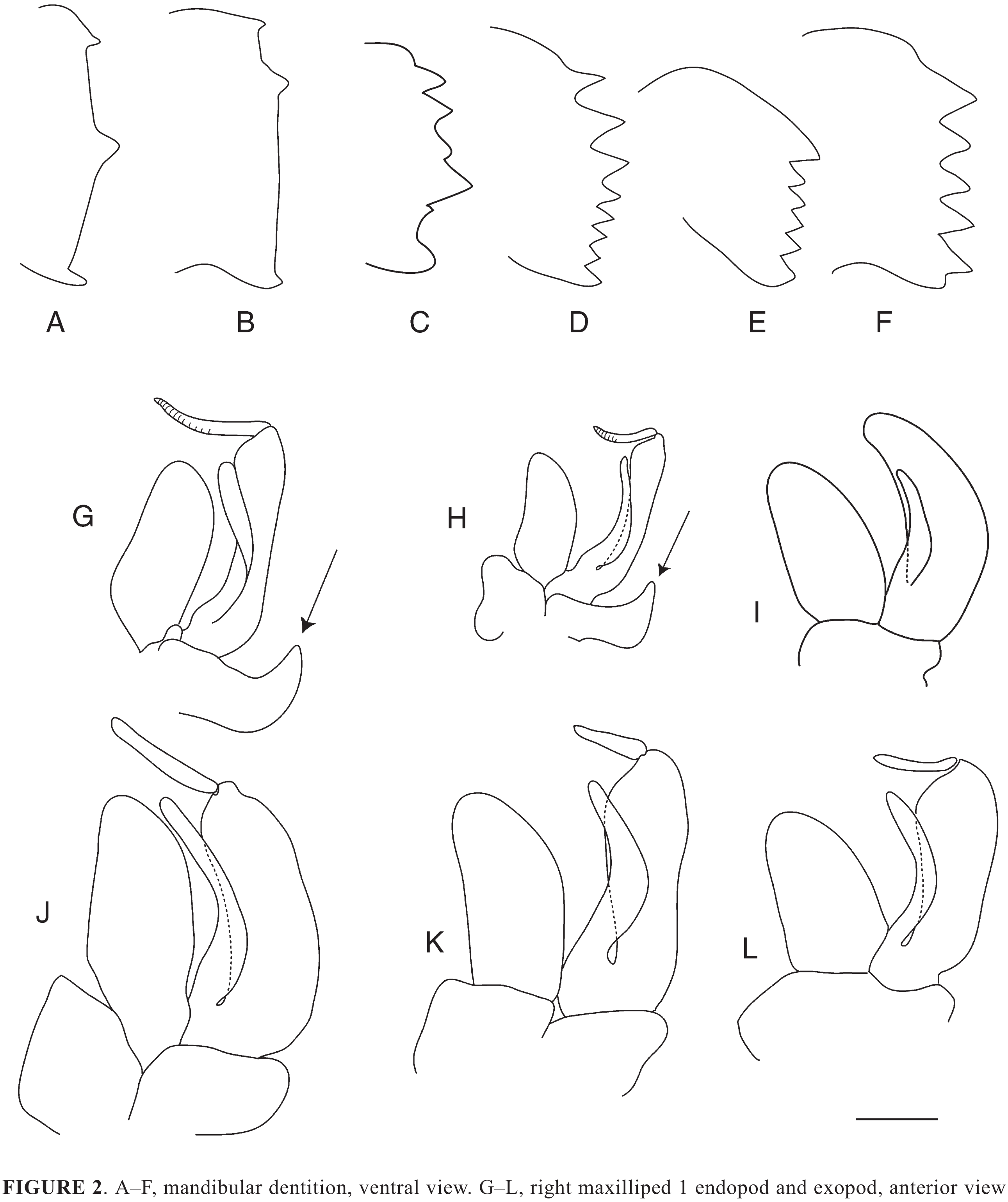

FIGURE 2. A–F, mandibular dentition, ventral view. G–L, right maxilliped 1 endopod and exopod, anterior view (epipod indicated by arrow). Eumunididae: A, G, *Eumunida australis* de Saint Laurent & Macpherson, 1990b (♂, pcl 12.9 mm, NMNZ Cr.21765); B, H, *Pseudomunida fragilis* Haig, 1979 (♀ ovig., pcl 20.5 mm, MNHN-Ga7507). Chirostylidae: C, I, *Chirostylus dolichopus* Ortmann, 1892 (♂, pcl 2.7 mm, MNHN station LA REUNION, MD32, CP172); D, J, *Gastroptychus rogeri* Baba, 2000 (♂, pcl 23.2 mm, NIWA 14555); E, K, *Uroptychodes epigaster* Baba, 2004 (♀, pcl 3.4 mm, NMNZ Cr.21766); F, L, *Uroptychus cardus* Ahyong & Poore, 2004 (♂, pcl 10.5 mm, NIWA 23086). Scale: A–F, not to scale; G, H, J, L = 1.00 mm; I, K = 0.45 mm.

Discussion

The family Eumunididae is readily distinguished morphologically from Chirostylidae *sensu stricto* in the presence of supraocular spines (absent in Chirostylidae), transverse carapace striae (absent in Chirostylidae), the presence of an epipod on maxilliped 1 (absent in Chirostylidae), unarmed antennular basal article, absence of male gonopods (present in Chirostylidae) and feebly rather than strongly dentate mandible (A. Milne-Edwards & Bouvier 1894; Haig 1979).

In the Chirostylidae *sensu stricto*, the mandibular cutting edge is strongly dentate along its length (Fig. 2C–F) whereas in the Eumunididae, the cutting edge is smooth apart from three teeth, one at either end, and a third tooth along the margin (Fig. 2A–B). A smooth or unidentate mandibular cutting edge is probably plesiomorphic in Anomura, being shared by most Paguroidea, all Galatheoidea, Hippoidea and the sister group to Anomura, Brachyura. In contrast, a dentate mandible appears to be a synapomorphy uniting Chirostylidae, Kiwaidae, Lomisidae and Aeglidae. As part of the Chirostyloidea, the eumunidids are nested within the chirostyloid + lomisoid + aegloid clade, indicating that the plesiomorphic condition of the mandibular cutting edge in the stem lineage Eumunididae is to be strongly dentate. Thus, the tridentate condition in the crown-group eumunidids, although superficially similar to that of paguroids, galatheoids and hippoids, is a derived state.

The enigmatic *Hapaloptyx* Stebbing, 1920 (type species *H. difficilis* Stebbing, 1920), is the only taxon for which we could not confirm morphological details. *Hapaloptyx difficilis* Stebbing, 1920, was described on the basis of an 8 mm pcl, disarticulated specimen collected off Natal, South Africa. It was in poor condition at the time of description, and was described as having a non-dentate mandible. According to Stebbing's (1920) figures, the chelipeds more closely resemble those of some majoid crabs than chirostylids, and we suspect that either the type account is inaccurate or that more than one species may comprise the type material. The body and other limbs otherwise correspond well to *Chirostylus*. *Hapaloptyx* requires redescription, but is retained in Chirostylidae at present.

The maxilliped 1 of the Eumunididae, in common with that of Kiwaidae, differs from Chirostylidae in having a well-developed epipod (absent in Chirostylidae) and a distally annulate flagellum on the exopod (non-annulate in Chirostylidae) (compare Fig. 2G, H and 2I–L). Note that the original account of *Kiwa* described the epipod as absent and exopod of maxilliped 1 as bilobed (Macpherson *et al.* 2005). However, we interpret the proximal lobe of the putative exopod described for *Kiwa* as the epipod; it corresponds positionally and structurally to the epipod of eumunidids, aeglids, hippoids and pylochelid hermit crabs.

The disposition of pleopods in male Chirostyloidea varies between families, but has not previously been summarized. In Chirostylidae, male pleopods 1 and 2 are present and pleopods 3–5 are vestigial or absent. In Kiwaidae, male pleopods 1–5 are all well developed. In Eumunididae, male pleopod 1 is always absent but the condition of pleopods 2–5 varies. Pleopods 2–5 are always absent in *Pseudomunida* and all but two species of *Eumunida*. In male *E. parva* de Saint Laurent & Macpherson, 1990a, and *E. smithii* Henderson, 1885, pleopod 2 is vestigial or absent, respectively, and pleopods 3–5 are all vestigial (Saint Laurent & Macpherson 1990a; Saint Laurent & Poupin 1996). The sequence of derivation of the male pleopods in Chirostyloidea is not immediately obvious. Near relatives of the Chirostyloidea (i.e., Aegloidea and Lomisoidea), however, have the following arrangement of male pleopods: in Aegloidea, pleopod 1 is absent and pleopods 2–5 are represented by a minute sclerite, the so-called pleopod remnant (Martin & Abele 1988), and in Lomisoidea, pleopods 1–2 are well developed, and pleopods 3–5 are minute as in Aeglidae, although not calcified (Pilgrim 1965). Based on these comparisons, loss of pleopods 3–5 appears to be plesiomorphic for Chirostyloidea.

Comparative studies of the sperm morphology of a wide range of anomurans indicated strong differences between representatives of *Uroptychus* and *Eumunida*, which also lend more support to the separation of the Chirostylidae and Eumunididae (Tudge 1997; Jamieson & Tudge 2001). Additionally, sperm characteristics of both taxa examined were more similar to hermit crab sperm morphology than to members of the Galatheidae and Porcellanidae.

Early larval morphology of *Eumunida* was examined for the first time by Guerao *et al.* (2006), finding clear differences between the first zoeas of *Eumunida* and other chirostylids. In particular, the larvae of

Eumunida did not show abbreviated development as in the other chirostylid genera (Clark & Ng 2008; Ogawa & Matsuzaki 1987; Pike & Wear 1969). As in other chirostylid larvae studied, the larvae of *Eumunida* were more similar to hermit and mole crab larvae than to those of the Galatheidae (Guerao *et al.* 2006). Both larval and spermatozoal studies thus support the hypothesis that chirostyloids are more closely related to hermit crabs than to galatheids (Ahyong *et al.* 2009; Chu *et al.* 2009; Schnabel *et al.* in press; Tsang *et al.* in press).

Pseudomunida, containing only *P. fragilis* Haig, 1979, is known from the Hawaiian Islands and the tropical western Pacific at 969–1480 m depth. *Eumunida* currently includes two subgenera, the nominate subgenus, with 17 species, and *Eumunidopsis*, with 12 species. Twenty-four of the 29 species of *Eumunida* occur in the western and central Pacific and three species each occur in Atlantic and Indian Ocean, at depths between 92–1320 m (Baba *et al.* 2008; Baba & Lin 2008). Notably, numerous records provide evidence of a close association between *Eumunida picta* Smith, 1883, and the scleractinian coral *Lophelia pertusa* (Linnaeus, 1758) in the northern Atlantic (Buhl-Mortensen & Mortensen 2004; Kilgour & Shirley 2008; Lessard-Pilon *et al.* 2010).

Although chirostyloids are highly speciose today, they are poorly represented in the fossil record. Schweitzer *et al.* (2010) listed two fossil species. The single fossil chirostylid, *Pristinaspina gelasina* Schweitzer & Feldmann, 2000 may correspond to the Chirostylidae. The second fossil species, *Protomunida pentacantha* Müller & Collins, 1991, was originally treated as a galatheid, but transferred to *Eumunida* by Schweitzer & Feldmann (2000) based on the five frontal carapace spines (rostrum and two pairs of supraorbitals) and transverse carapace grooves. We suggest, however, that Müller & Collins' (1991) species is actually a galatheoid in the genus *Sadayoshia* Baba, 1969, which it closely resembles, not only in the conformation of the frontal spines, but in the presence of five marginal carapace spines behind the cervical groove, presence of a transverse row of epigastric spines, and the series of postcervical spines on the carapace surface (present in several species of *Sadayoshia*). *Sadayoshia pentacantha* **comb. nov.** is known from coral rich Upper Eocene (Priabonian) strata Hungary and Italy, and represents the first appearance of the genus in the fossil record. Thus, at present, the palaeontological record of Chirostylidae is restricted to *Pristinaspina gelasina*; Eumunididae and Kiwaidae are as yet unknown from fossils.

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